ECOSYSTEM RESEARCH IN THE TROPICS

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Perhaps the biggest problem when discussing ecosystem research is, just what is ecosystem research, and how does it differ from other branches of biology? A traditional definition of ecology is that it is the study of interactions between organism and environment. Platt (1974) and Jordan (1975) have argued that this definition is inadequate, because a large portion of all biological and agricultural research and a significant fraction of medical and engineering studies can be construed to be studies of the interaction between organism and environment, whether or not the studies are really ecological. For example, a sewage engineer might convince a local town council that he is an ecologist because he studies interaction between bacterial concentrations and river flow, and therefore he could claim competence to prepare an environmental impact statement on the effect of sewage outfalls from new housing developments on the stream that passes through the town. We would argue that he is not competent because ecological problems resulting from sewage disposal are not limited to bacterial concentrations, but include such phenomena as eutrophication and resulting changes in fish populations, and recreational and economic use of the unpolluted river.

If "the study of interactions between organisms and environment" is an inadequate definition of ecology, because many diverse types of scientists study such interactions, what then is the unit of study that is unique or basic to ecology? One system of classifying units of biology is the hierarchical approach. In this system, for example, the basic unit of study for cytologists is the cell, and the basic unit of study for the morphologist is the organ. For ecologists, the basic but it must have definable limits inside of which there are integrated functions. ecosystems."

If our definition of ecology is "the study of ecosystems," we must then define ecosystems. An ecosystem is an integrated unit, consisting of interacting plants and animals whose survival depends upon the maintenance of biotic and abiotic structures and functions. The unit does not necessarily have to be isolated, but it must have definable limits inside of which there are integrated functions. What are these ecosystem functions?

There are three functions upon which ecosystem ecologists focus their attention: energy flow; nutrient cycling; and water flux. Nutrients, energy, and water also are studied by physiologists, but what sets ecosystem ecology apart is the structure that supports these functions. Physiologists study flows of energy, nutrients, and water in individual organisms, whereas ecologists study them on an ecosystem scale.

In using this definition of ecology we do not mean to say that the only truly ecological studies are those which follow energy, nutrients, and water through

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ecosystems. We certainly do not exclude those scientists who focus on species interactions and population dynamics. What is important is that the investigator maintains a holistic perspective.

Maintaining a holistic or ecosystem perspective, in the sense that the scientist considers all ecosystem aspects, is what sets an ecologist apart from scientists of other disciplines. For example, if we see a scientist studying the aquatic life in a river close to a sewage outfall, we could tell if he has the ecological perspective by asking him his objectives. If he answers that he is trying to protect human health by getting rid of harmful bacteria, he may be an environmental scientist, but he is not an ecologist because he is not considering all the ecological effects of the sewage entering the river. If he answers, in effect, that he is trying to protect human health by keeping man's life support systems functioning, in this case perhaps by preventing eutrophication and thereby maintaining a downstream fishing industry, he has the ecological perspective. He considers the implications of the problem, above and beyond the direct and obvious problem.

A Tropical Ecological Hypothesis

Because the title of this symposium is "Perspectives in Tropical Botany," we should relate tropical botany to ecosystem research in the tropics. Tropical plants are, of course, the base of the food chain in tropical ecosystems. Tropical plants also recycle nutrients from decomposing organic matter on the forest floor and make the nutrients available to the animals. It is in this sense that we tie tropical botany to tropical ecology.

We are going to talk mainly about our own ecosystem project in the tropics, but we will place it in perspective by comparing it with other tropical ecosystem research projects. The overall objective of our project is to study the structure and function of an Amazonian rain forest, so that increased ecological understanding of the ecosystem can contribute to more effective applied management in future years. However, we are not interested only in the applied aspects, we are interested in the basic nature of Amazonian ecosystems, what temperate-zone man expected to find there, what he actually found, and how the differences can be explained in terms of ecosystems theory.

Temperate-zone man has equated tall forests and large trees, and diverse flora and fauna with productive landscapes. When he encountered the Amazonian rain forest, he was impressed by the mass of vegetation and variety of organisms, both of which exceeded his temperate experience. He concluded that the tropics must be very productive. However, when he converted tropical forests to agricultural plantations, yield declined drastically. Why?

Temperate experience suggested that the yield was related to soil fertility. Therefore, the problem must be in tropical soils. And indeed, the amounts of essential nutrients could be very low. But then, how could luxurious tropical forests survive on such poor soils?

Ecologists have hypothesized that development and survival of lowland tropical rain forest is through nutrient-conserving mechanisms that maintain the essential elements within the biomass of undisturbed forests, and that the destruction of these mechanisms by cut-and-burn agriculture results in rapid loss of nutrients, with a resultant loss in ecosystem productivity. While this concept is almost popular knowledge, the hypothesis has never been tested. The major emphasis of our Amazonian ecosystem research program is to test this hypothesis and to identify the nutrient conserving mechanisms which operate in the undisturbed tropical forest ecosystem.

THE SAN CARLOS PROJECT

The field site of our project is near San Carlos de Río Negro, in Amazonas Territory of Venezuela. The site is within the north-central drainage basin of the Amazon River. There are two principal forest types in the area, both about equally important in terms of area. One is the tierra firma forest, located on laterite covered with a thin layer of sand or gravel. Species diversity is high, and biomass is close to 400 t/ha (Jordan & Uhl, in preparation). The other type is located on sand, with a podsol B horizon at about one meter depth. During heavy rains, the water table reaches the soil surface in this type. Biomass and species diversity is less than on the tierra firma site (Klinge, 1976).

The experimental approach is as follows: We have a series of experimental and control plots on both soil types. We have measured the nutrient inputs, outputs, storages, and transfers of the major ecosystem compartments in these plots for one year. After one year, the experimental plots were cut and burned following the traditional local practices. In the podsol site, some areas were planted to rubber plantation and others were abandoned for secondary succession studies. In the tierra firma site, the experimental area was planted with typical crops of the area, manioc, pineapple, plantain, and a few other species.

As a result of our observations and measurements during the first three years of the project, it has become apparent that a well-developed root mat and humus layer which occurs on top of the soil surface plays a key role in nutrient conservation and recycling. We hypothesize that:

(1.) The root mat and humus layer on the forest floor act as an exchange column to prevent leaching of nutrients until the nutrients can be taken up by the roots.

(2.) Mycorrhizal fungi play a role in the direct transfer of nutrients from decomposing litter to roots.

Other nutrient conserving mechanisms that we are examining are:

(3.) Algae and lichens living on the surfaces of leaves and bark play an important role in nitrogen fixation of the forest.

(4.) There are virtually no nitrifying bacteria in the forest. Maintenance of nitrogen in the ammonium form is a nitrogen conserving mechanism (Rice & Pancholy, 1972).

(5.) There is either a sulfur fixing capability in the forest such as sulfur fixing bacteria, or the forest is being depleted of sulfur, since loss of sulfur through stream flow far exceeds input through rainfall.

(6.) Sclerophylly and evergreenness in the tropical rain forest are nutrient conserving mechanisms.

(7.) Many nutrients move from leaves back into the stems before the leaves fall.

(8.) Trees are adapted to the oligotrophic environment in that roots are physiologically very efficient in extracting nutrients, utilize a low oxygen environment, and, at least in the podsol site, are resistant to flooding.

(9.) Insect predation of leaves is low in the podsol site, and only slightly higher in the laterite site. These low predation rates may be due to plant compounds such as alkaloids and polyphenols. These compounds may act as nutrient conserving devices in that it is more economical for the plant to manufacture secondary compounds than it is to manufacture a new leaf in the nutrient poor environment.

(10.) Termites play an important role in redistribution of nutrients in the forest.

(11.) In the tierra firma site, the rough root mat on the soil surface causes the newly fallen leaves to lie at various vertical angles, with the result that the leaves resemble somewhat the shingles on a pitched roof. Rainfall and throughfall quickly pass over these "shingles," minimizing the opportunity for leaching by water, and allowing more time for recycling by mechanisms such as mycorrhiza.

Other hypotheses are emerging relevant to the treated experimental areas:

(12.) Despite the fact that the roots of secondary successional species are primarily in the upper layer of mineral soil and not on the soil surface, they have an extremely high capacity for nutrient uptake. When the forest is cut, but allowed to immediately begin the successional process, the successional species can recover a large proportion of the nutrients released by the decaying organic matter. However, if the ecosystem is cropped, most of the nutrients will be lost, either through leaching or through harvesting.

(13.) Life spans of slash and burn farms are determined primarily by the decay rate of organic matter and root biomass in the soil which supplies nutrients to the crops.

In addition to development of these ideas, comparison of the data from the two forest types with different soil conditions has led to hypotheses regarding nutrient cycling in the podsol sites versus the lateritic sites, as well as hypotheses regarding cycling in these ecosystems compared to other forest ecosystems:

(14.) In the laterite sites, standing crop, productivity, and rates of nutrient cycles are slightly higher than in the podsol, seasonally flooded site, possibly due to lesser extremes of water conditions and anaerobiosis.

(15.) Highly sclerophyllous vegetation with highly inclined leaves located in patches on the podzolic soils, with a xerophytic aspect, reflect an extreme where there occurs drastic alternations between drought conditions and flooding with anaerobic conditions.

(16.) Consumption of vegetation by insects in the podsol site is lower than in the laterite site.

(17.) In both sites, rates of productivity and nutrient cycling are lower than on more fertile soils in both temperate and tropical regions.

(18.) Although biomass in both sites is relatively low in comparison with other forests, the forests are climax in the sense that net ecosystem productivity is zero.

(19.) The biomass of the forest is limited by the available pool of nutrients and the capability of nutrient-retaining mechanisms to prevent their loss.

Other relationships that have emerged as a result of our studies of water balance and biomass, which were necessary steps in the quantification of the nutrient budget, are:

(20.) Rate of transpiration in trees is independent of species and site, and depends only on sapwood area per unit of forest floor.

(21.) Biomass of all tree species can be described by a single regression on (diameter)^2 (height) (density).

Organizational Aspects

The San Carlos project is a cooperative study between institutions in Venezuela, the United States and Germany. The project is headquartered at Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (I.V.I.C.), in Caracas, Venezuela. Other participating Venezuelan institutions are Universidad Central de Venezuela, and CODESUR, a branch of the Ministry of the Environment. The German participating institutions are the Max Planck Institute at Plön, and the World Institute of Forestry at Reinbeck (Hamburg). Participation of United States institutions is being coordinated through the Institute of Ecology, University of Georgia.

Funds for the project are coming from the Organization of American States (OAS), UNESCO, CONICIT (Venezuelan Science Foundation), United States National Science Foundation, Deutsche Forschungsgemeneinschaft, and indirectly through IVIC and CODESUR.

The project has been designated a MAB I pilot project by UNESCO because of the progress that has been made in relation to other MAB ecosystem studies in the tropics. It is also part of the Humid Tropics Forest Project of the OAS, which includes projects in Brazil, Trinidad, and Colombia.

The project was started in 1974, at just about the time the International Biological Program (IBP) Biome studies were drawing to a close. In designing the project, we strove to take advantage of the lessons learned during the operation of the IBP studies. The strengths and weaknesses of these programs have been discussed by Mitchell et al. (1976).

In order to build upon the wisdom gained from the IBP studies, we did the following:

(1.) First of all, we returned to the old-fashioned method of designing the project, to test hypotheses, rather than build the project around a technique, such as was done with systems analysis in the IBP studies.

(2.) Secondly, we confined our ecosystem model to a single process model, rather than model many processes and populations and attempt to integrate them into a single model, as had been done with little sucess in the IBP studies.

(3.) Thirdly, we kept the project small, in comparison with the United

States IBP studies. In many cases, the large scale of these studies had caused them to be unwieldy from the point of view of management.

Another organizational factor which weighs heavily in biological research in the tropics, and especially ecosystem research because of its magnitude, is the problem of scientific imperialism. For many decades, if not for centuries, North American, European, and Japanese scientists have visited Latin American, African, and Southeast Asian countries, collected data, specimens, and samples, brought them back to their home countries, and bestowed little or no scientific benefits upon the host countries. Over the years, this has resulted in a resentment in the tropical host countries because knowledge derived from such studies or whole efforts did not contribute to the improvement of personnel and infrastructure in the respective countries, and did not aid the development of similar projects run by their own people. Many times it has been due to lack of local scientific personnel, but often the projects did not have the policy of improvement of local capabilities (Budowski).

This problem was discussed during the 1973 Costa Rican meeting of tropical ecologists, during which ecosystem research in the tropics was evaluated and recommendations for future research was discussed. The proceedings of this conference were later published in the book *Fragile Ecosystems* (Farnworth & Golley, 1973).

As a result of the recommendations in this book, our ecosystem project was specifically designed to contribute to the scientific infrastructure of the host country. For example, instead of bringing samples back to the United States or Germany for analysis, we have set up our own analytical laboratory in Caracas, and trained a team of technicians to operate it. Part of the data processing is taking place in Caracas, but copies of all original data are kept in Caracas, so that it can be used by other investigators.

We have limited the number of North American and European visitors, with the intention to increase as much as possible the number of Latin American participants. Further, we make an effort to have counterparts for visiting scientists, so that the visitors experience will not be lost to Venezuela. For example, we have initiated a soil microbiology program, in which the visiting United States microbiologist is traning a Venezuelan investigator to follow through and complete a study of nitrifying bacteria in the Amazon forest.

COMPARISON WITH OTHER ECOSYSTEM STUDIES

In general, most of the values of the ecosystem parameters which we have obtained so far are equal to or somewhat lower than values from other tropical ecosystem studies.

Total living biomass on the tierra firma sites near San Carlos averaged 391 t/ha. Other biomass studies of tropical rain forests have produced values within the same range or somewhat higher. In Puerto Rico, Jordan (1971) estimated the biomass of one site of a montane forest to be 228 t/ha, while Ovington & Olson (1970) estimated three in the vicinity to be 324, 209, and 269 t/ha. Dry weight of above ground biomass in two Panama forests were 377 and 276 t/ha (Golley et al., 1975). In Ghana, Greenland & Kowal (1960) estimated biomass of a secondary forest to be 289 t/ha, while two evergreen tropical forests in the Ivory Coast, constituting part of the French project at the Banco and Yapo reserves, were estimated to have above ground biomasses of 465 and 425 t/ha (Huttell & Bernhard-Reversat, 1975). In the Pasoh forest of Malaya, above ground dry weight of biomass was 664 and 475 t/ha on two plots (Kato et al., 1974), considerably greater than our values for San Carlos. In evergreen seasonal forests of Cambodia, total biomass in two stands was 415 and 348 t/ha, (Hozumi et al., 1969), while in Thailand values ranged from 326 to 404 t/ha (Ogawa et al., 1965).

Near Manaus, Brazil, Klinge & Rodríguez (1973) found about 900 t/ha fresh weight including roots. If we assume the moisture percentage is the same as in San Carlos, then total dry weight would be 585 t/ha. Rodin & Bazilevich (1967) in their survey of global biomass put an average value for tropical forests greater than 500 t/ha. The world biomass summary by Art & Marks (1971) gives similar high values.

Leaf fall values which for the San Carlos forest are around 5 t/ha/yr are in the low part of the range of values for tropical forests. For example, in the Ivory Coast Forest Project, leaf fall rates were 8–10 t/ha/yr (Huttel, 1975) and in the Khao Chong forest, Thailand, rates were about 12 t/ha/yr (Kira et al., 1967). In the eastern Amazon Basin, near Belém, rates were 7.4–10.7 t/ha/yr, but in the central basin near Manaus, the rate was 6.7 t/ha/yr (Klinge, 1974), only slightly greater than the value for San Carlos. Jordan & Murphy (1977) have presented litter fall values from 27 tropical forests. Most values are greater than 7 t/ha/yr, and there are quite a few values greater than 10 t/ha/yr.

Rates of soil respiration at San Carlos are about 400–500 mg C/m^2/hr, within the range encountered in Thailand.

Concentrations of nutrients in water fluxes such as throughfall, stem flow, and soil water are generally less than were found in tropical forests in Puerto Rico (Jordan, 1968), Panama (Golley et al., 1975), and Ghana (Nye, 1961).

The most striking difference between our study, those of Klinge (1973), those of Went & Stark (1968)—all in the Amazon Basin—and those studies in other regions of the tropics is the apparent importance of the root mat and humus layer in the Amazon forests. As we mentioned previously, the root mat appears to play a key role in the recycling of nutrients. Yet in other studies outside the Amazon region, the presence of a surface mat, if present, is not noted or emphasized.

The evidence that we are obtaining, then, is verifying the idea that the Amazon forest is severely nutrient limited, and that low biomass, low litter fall, and low nutrient concentrations, all are adaptations to the oligotrophic condition. In addition, mechanisms such as the above-ground root mat and direct recycling by mycorrhiza are adaptations to help the ecosystem survive in the nutrient-poor conditions. The implication is that destruction of the Amazon forest on a large scale will cause an irretrievable loss of nutrients and consequently of the ecosystem, because large scale clearing destroys the nutrient conserving mechanisms.

FUTURE TROPICAL ECOSYSTEM WORK

What about future ecosystem research in the tropics? It is typical for a presentation to conclude with a plea that it is especially important for the particular research discussed to receive more recognition and greater support. We will not break with this tradition.

In general, ecosystem research in the tropics is too fragmented, with the result that the studies do not have the political effectiveness that they should, in the sense that the results of ecosystem research should influence political planning for a region. When a group of scientists work together on a single ecosystem problem, such as they did on the Hubbard Brook study (Bormann et al., 1968), the final impact is much greater, even if the findings are very controversial as they were in the Hubbard Brook study (Aubertin & Patric, 1974). For this reason then, we make the plea for less fragmented research and more integrated efforts, with the ecosystem approach being a natural integrating device.

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